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POPULATION ECOLOGY OF THE GYPSY MOTH

PORTHETRIA DISPAR L. (Lepidoptera: Lymantridae)

by Henry A. Bess

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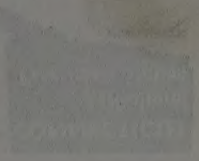

FOREWORD

The Connecticut Agricultural Experiment Station is pleased to publish the manuscript by Doctor Bess on the gypsy moth, perhaps the most destructive and certainly the most dramatic insect in Connecticut. The bulletin is published with funds provided by the Lockwood Trust, a fund set up many years ago to encourage biological research and "to disseminate the results thereof."

Connecticut has had an unusually large stake in the investigations. For many years, the gypsy moth had caused less damage east of the Connecticut River than west of it. The study accorded an opportunity to determine the reasons for the difference and to forecast the outbreaks west of the river.

During the course of the research, our entomologists, especially Dr. R. B. Friend, cooperated with Dr. Bess in many ways. Using the methods developed by Bess, Friend was able to forecast the massive outbreak of gypsy moth in 1953-54 in Granby.

This study covered a period of eight years during which serious defoliation occurred over large areas. Some parts of the work have been published and are cited in the bibliography. This present report completes presentation of the data, and the discussion and conclusions represent the mature judgment of the author. It is therefore especially useful as a starting point for the further studies necessary for a more complete understanding of the problem.

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POPULATION ECOLOGY OF THE GYPSY MOTH *PORTHETRIA DISPAR* L. (Lepidoptera: Lymantridae)

by Henry A. Bess[1]

INTRODUCTION

The gypsy moth, *Porthetria dispar* L., is widely distributed in the northeastern United States and in some localities widespread defoliation occurs annually while in others the moth is extremely scarce or absent. During the period between 1937 and 1945 intensive studies were made under a wide range of woodland conditions to determine the favorable and unfavorable ecological conditions for this defoliator to reach or maintain itself at a sufficiently high population level to cause noticeable defoliation of trees, determine the relative importance of different natural control factors in the different regions of abundance, and to develop feasible forest practices for reducing the gypsy moth hazard where it was a menace. It was hoped to discover whether the insect is likely to eventually become persistently abundant in the oak forests of Connecticut, western Massachusetts and eastern New York, or if there is a good likelihood that natural control factors will continue to hold it in check below the density necessary to cause widespread defoliation. Furthermore, it was desirable to find out what types of forest growth found in the infested parts of New York, Pennsylvania and western and southern New England are the most susceptible to the insect, so that the most efficient use can be made of personnel and equipment available for suppressing the moth in these outlying regions.

Concrete data were sought on a number of relationships: population density and sex ratio, population density and egg production per adult female, population density and increase or decrease, population density and degree of defoliation, population density and parasite, predator, and disease abundance, forest ecological conditions and abundance of the gypsy moth and its various enemies.

Originally it was planned that the study would be carried on intensively for a period of at least 10 years. Emphasis was placed on the need of getting as much information as possible on the quantitative mortality produced by various natural control factors in both increasing and decreasing populations.

Certain applied aspects of the study have been published and recommendations made for the use of foresters in the region where the insect is a pest (Bess *et al.*, 1947).

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[1] At present the author is Senior Entomologist, Hawaii Agricultural Experiment Station, Honolulu. During the progress of the research he was entomologist of the United States Department of Agriculture, located in New Haven, Connecticut, near The Connecticut Agricultural Experiment Station.

The author is grateful for the cooperation of Dr. R. B. Friend and other members of the staff of The Connecticut Agricultural Experiment Station.

REVIEW OF LITERATURE

Geographical Distribution

The original home of *P. dispar* was probably southeastern Asia (Goldschmidt, 1933). It now inhabits a considerable part of the Palearctic region, and several thousands of square miles in the northeastern part of the United States. The species is found throughout central and southern Europe but does not occur north of Stockholm in the Scandinavian countries, or in the northernmost part of Russia. To the east the insect occurs in the Caucasus Mountains, Russian Turkestan, the Altai Mountains in Mongolia, northern China, and Japan. At the eastern edge of the Eurasian continent it is found as far north as the Amur River in Siberia and as far south as Shanghai.

How and when the moth reached Europe is unknown but it was introduced into Massachusetts from France by Leopold Trouvelot in 1868 or 1869 (Forbush and Fernald, 1896).

General Abundance

For many years the gypsy moth has defoliated large acreages of woodland annually in Europe and North America. However, there are regions both in Europe and North America, where, even though the insect is present, it has seldom or never become sufficiently abundant to cause conspicuous defoliation. As an outgrowth of the present study it has been pointed out that in North America abundance and frequency of outbreaks have been closely associated with ecological regions or forest and site conditions (Bess *et al.*, 1947).

There are numerous records of the gypsy moth defoliating trees and causing economic damage throughout the central and southern parts of Russia. Apparently in Japan it is of relatively little economic importance as is evidenced by the statement, ". . . the Japanese gypsy moth is pretty thoroughly controlled through natural agencies. . . ." (Howard and Fiske, 1911.) However, recently, 1953-55, widespread defoliation occurred in northern Japan. The scarcity of the insect in England has been publicized and commented on by many observers (Forbush and Fernald, 1896; Goldschmidt, 1933). During the last half of the 19th century the moth was rare there at times and at other times sufficiently abundant to damage gardens and woodlands. The consensus seems to be that the moth began to gradually disappear about the middle of the 19th century and is now rare or extinct in England. However, it still reaches epidemic populations in central and southern Europe, and in Algeria and Morocco it has been abundant locally.

As early as 1880 the gypsy moth was abundant in the immediate vicinity of Trouvelot's former residence in Medford, Massachusetts, where the insect accidentally escaped approximately 10 years earlier. During the next 8 years it continued to be a public nuisance within that immediate section of the town. From 1889 to 1897 an energetic effort was made to eradicate the insect but defoliation occurred in several of the 30 townships known to be infested. There was little defoliation in

1898 and 1899, and control work was discontinued in 1900. However, 2 years later defoliation occurred again, and in 1905 control work was resumed on a "suppression basis." Subsequently, it was found that there were 300 square miles "thickly infested" and about 2,000 square miles "lightly infested" in Massachusetts. An energetic program was adopted to suppress the moth and keep it from spreading but the work did no more than '. . . slightly retard the continued spread of the pest" (Burgess and Baker, 1938).

During the past 4 decades the moth has been persistently abundant throughout a large area in eastern New England, defoliating thousands of acres of woodland annually. However, over a considerable part of the infested region the insect has never become sufficiently abundant to defoliate trees, but can usually be found if diligent search is made for it.

Natural Control

Forbush and Fernald (1896) published a large volume in which Fernald reviewed the earlier literature on the gypsy moth and presented information obtained on the natural enemies of the insect in the early nineties in Massachusetts. Fifteen years later, after extensive work had been done on the importation of parasites from Europe and Japan, Howard and Fiske (1911) published another large volume in which they discussed the natural enemies of the moth in various parts of the world, including the United States. Burgess and Crossman (1929) summarized the parasite importation work and Schedl (1936) subsequently published a lengthy review of the literature on the gypsy moth. In addition, a number of excellent scientific papers on the biologies of various gypsy moth parasites have been published in the United States. A brief resumé of some of the highlights and opinions on the natural control of the moth are given below.

In the early nineties entomologists were discussing the question of why the gypsy moth had become extinct in England where it had become established at least 150 years before. Dr. Fernald (Forbush and Fernald, 1896) called attention to the humid climate of England and the darker color of foliage and arboreal animals in England than in central Europe and eastern United States. He raised the question as to whether the darker color of the foliage and other surroundings may not have rendered the female moths more conspicuous objects to their enemies, so that in the struggle for existence the species was exterminated.

Prior to 1900 entomologists in Europe recommended the protection of gypsy moth enemies, including bats, cuckoos, starlings, crows, titmice, tree creepers, ichneumons and tachinids. Forbush and his assistants made numerous studies on the destruction of the gypsy moth by birds and concluded that they played a very important part in the destruction of it in Massachusetts. Fernald reported that skunks, frogs, toads, spiders, mites, flies, beetles, ants, wasps, hornets and hymenopterous parasites destroyed numbers of the gypsy moth. He stated in 1891 that the insect was generally held in check by its natural enemies in Europe but he did not claim that the enemies attacking the insect in Massachusetts were a factor of great importance in the suppression of the pest.

Howard and Fiske's famous Bulletin No. 91 appeared in 1911, 6 years after the beginning of the importation of parasites into the United States.

During this period many observations had been made on the destruction of the moth in Europe by different enemies. In several instances the entomologists were convinced that parasites accounted for large enough proportions of the insect to bring it under control. They stated that, ". . . the Japanese gypsy moth is pretty thoroughly controlled through natural agencies, and among these parasites appear to rank very high." Observations in Russia revealed that in some localities parasites were very abundant, while in others they were extremely scarce. In certain heavily defoliated forests the "wilt" disease killed vast hordes of larvae and pupae, but the entomologists were convinced that the disease was of little value as a control agent. In France, several species of parasites were found but apparently only in small numbers. However, they observed that the moth was not found in large numbers within the rich and well-watered bottom lands, but that enormous numbers of caterpillars were collected from ". . . the chapparal covered, arid, and uncultivated elevations . . ." In the United States the introduced predacious beetle, *Calosoma sycophanta* L., and certain parasites were already established and showing promise of becoming valuable in the control of the pest.

For decades it has been observed that low winter temperatures frequently destroy many gypsy moth eggs, especially in the interior of New England. Summers (1922) concluded that exposure to a temperature between —20° to —25°F. will kill all eggs.

In 1913 Fiske (1913) called attention to the probable importance of the abundance of oaks and other favored food species to the abundance of the moth. Subsequently considerable study was made along that line, and more recently other writers have recommended the elimination or reduction of the proportion of favored food species as a means of gypsy moth control (Behre, Cline and Baker, 1936; Brown and Sheals, 1944). However, these writers also recognized that natural control factors had held the insect under control for many years in the oak woodlands of Connecticut. In 1947 Bess, Spurr and Littlefield (1947) reported that gypsy moth abundance in the Northeast had been closely associated with forest and site conditions, and recommended forest practices to reduce the gypsy moth hazard in areas where it is a menace. These practices would be good silviculture even if the gypsy moth was not present.

Bionomics

There are 4 primary developmental stages of the gypsy moth—egg, larva, pupa, and adult. It is a univoltine species. Most of the eggs are deposited in July, embryonic development is completed within a few weeks, and the larvae hibernate within the eggs. Hatching may begin the latter part of April but most eggs hatch in May. There are usually either 5 or 6 larval instars; 5 in case the individual is male and 6 if female. Pupation begins the latter part of June and most adults emerge by mid-July.

The male moths are strong fliers but the females seldom or never fly, even though they have fully developed wings. The abdomens of the females contain large numbers of eggs, weighing them down to the extent that flight appears practically impossible. On emergence the females seldom crawl more than a few inches away from the empty

pupal cases. Within a few hours after emergence a chemical sex attractant is ejected which attracts male moths for a distance of more than a mile. Soon after copulation oviposition occurs and usually each moth deposits all of her eggs in a single mass. Frequently the moths die without leaving their newly deposited egg masses.

At the time of hatching, young larvae may remain on the egg masses for 2 or 3 days, or even a week, depending upon meteorological conditions. According to Fernald (1896), the first food eaten is leaf hairs. However, they soon cut small holes in young leaves and also feed along the periphery of the leaves. The larvae spin silken threads and many are often seen dangling in the air by these threads. This spinning habit results in considerable dispersion of small larvae by wind. A resident on Cape Cod told me that one spring he was painting his house at the time large numbers of small larvae were in the air and the side of the house became coated with larvae to such an extent that at a distance one was unable to determine the color of paint used. The nearest woodland was 200 to 300 yards from the house. This meant that there were literally thousands of larvae in the air. Many studies have been made which revealed that small larvae were transported for several miles by the wind.

Feeding is normally done at night but a small proportion of the larvae ingest some foliage during the day time. The larvae tend to rest in concealed places during the day and also molt in such places. When the larvae are small, suitable resting and molting niches are usually found under small pieces of loose bark on dead twigs, in crevices on the limbs near the foliage, and even on the underside of green leaves. In good mesophytic hardwood stands larger larvae tend to descend the trees at dawn and take shelter in the litter on the forest floor. However, if there are suitable niches above the forest floor, such as large pieces of loose bark, tree cavities, etc., many of these larger larvae rest during the day and molt within such niches. In open, dry woodlands where there is practically no loose litter on the ground, or the litter is exposed to the direct sunlight and becomes very hot, large larvae usually remain above the forest floor, frequently resting and molting in the green foliage. Pupation occurs in niches similar to those where the larger larvae are found during the daytime.

A tremendous amount of genetical work has been done with the gypsy moth. Goldschmidt (1933) found that by crossing a certain European variety with a Japanese variety, intersexes (hermaphrodites or gynandromorphs) were produced. This led to an exhaustive study of racial variations in intersexuality and their geographic distribution. On the basis of his breeding work he classified the geographic races as very weak, weak, half-weak, neutral, and strong, depending upon the intersexes of the offspring. He states that, "A male of a strong race produces with a weak female only sons, with a half-weak female only intersexual daughters of a definite degree, and with a neutral or strong female only normal offspring." He concluded that ". . . the different sex races are in some way in harmony, not with individual climatic factors, but with the character of the whole seasonal cycle in the respective region." His studies show that there are a number of individual processes of growth and differentiation which are typically different in geographic races. For example, there are differences in length of

larval period, velocity of differentiation of gonads, number of larval instars, length of diapause and the color and markings of larvae and moths in different geographic races. According to Bodenheimer (1938), Goldschmidt is inclined to believe that each race ". . . is fitted genetically in the specific climatic cycle of its natural habitat by small hereditary changes in the degree of cold necessary for breaking the diapause and the thermal constant."

Gypsy moth larvae feed on a wide variety of plant species but they show a preference for some species over others, both in the laboratory and field. In later instars they can utilize a larger variety of plants as food than in earlier instars. Extensive laboratory experiments and numerous field observations have been made to determine food preferences of the larvae in New England. Mosher (1913) and more recently Burgess and Baker (1938) classified many New England forest trees and plants on the basis of their favorability to gypsy moth larvae.

INVESTIGATION METHODS

These ecological studies were essentially quantitative population studies of both the host and its natural enemies, designed to be carried out intensively for a period of several years. An attempt was made to develop and use methods which would give statistically reliable estimates of the populations measured, the mortality that occurred in the different developmental stages, and that produced by various factors. As would be expected, practically all estimates of population density, mortality, survival, defoliation, and forest composition were based on samples. These were taken either at random or in a planned systematic manner so that the factor of bias in procuring them was kept at a minimum. When feasible, an adequate number of samples was taken to obtain statistically reliable estimates above the 90 per cent level; however, this was not always possible.

Establishment of Experimental Areas

In the selection of the specific study areas, woodlands were sought which were characteristic in general of the regions in which they were located. All of those selected had one or more stands highly favorable to the moth from the standpoint of species composition. Most of the areas contained a preponderance of oak, but each also usually had one or more stands or pockets composed of other favorable food species. At the time of establishment all of the study areas were known to be infested and most of them had been known to support a relatively high population of the moth for the zone.

Two major work centers for intensive population and mortality studies were established; one at Petersham in central Massachusetts and the other at Freetown in southeastern Massachusetts. In Petersham the minimum populations of the moth had been sufficiently high for it to be found with diligent search during endemic years but widespread defoliation had seldom occurred during the preceding 30 years, while

in Freetown widespread defoliation had occurred within the township practically every year for 20 years. In addition to these 2 major study centers, similar intensive population and mortality studies were made in special plots in Woodstock, Connecticut; Alfred, Maine; and Wendell, Massachusetts, for a part of the period. Furthermore, studies of a less intensive nature were made in supplementary experimental areas selected on the same basis at Hillsborough, New Hampshire; Brewster, Northampton, North Reading, and Spencer, Massachusetts; Burrillville, Rhode Island; Eastford and Granby, Connecticut; Canaan and Hillsdale, New York; Jenkins and Pittston, Pennsylvania. A special effort was made to procure data from a few localities where the insect was never abundant, and in all study areas in years when the population receded to a low level. Data obtained at extremely low population densities were often unsatisfactory statistically, but they furnished useful information on the population dynamics of the species.

Larger Experimental Areas

The experimental areas were usually between 50 and 100 acres in size, with some diversity in stand composition and general ecological conditions. During the first years of study the areas in use were carefully mapped to show stand and sub-stand lines based primarily on composition. As the study progressed these maps were considered inadequate, since the information procured indicated that gypsy moth abundance was more closely associated with certain forest and site conditions related to site values and stand history than to composition. Therefore, general assessments were also made of the site values and ecological conditions suspected of being associated with gypsy moth abundance.

Intensive Study Plots

A series of 2 to 4 one-fifth acre square plots was usually established in each area where quantitative measurements were made of the population and mortality in each developmental stage. Each plot was located within a relatively uniform middle-aged stand 6 acres or larger in size and free of stonewalls and excessive debris. Each plot was divided into 36 squares (15.5′ × 15.5′), and permanent stakes set to indicate the divisions. For the duration of the larval period, usually from about May 1 to July 31, a standard weather instrument shed was kept in the center of one of the plots at each study area and a continuous recording hygrothermograph maintained within it. In addition, in or near each plot records on precipitation, maximum and minimum temperatures, wet and dry bulb temperatures, and the evaporation from a pair of Livingston porous spheres were taken each morning between 8:00 and 9:00 o'clock. Estimates of the larval mortality were also obtained daily throughout this period in the manner described later.

Supplementary Plots

Two or more supplementary plots, one-tenth acre in size and circular in shape, were established in each experimental area, with the exception of the one at Granby, Connecticut, where 13 one-acre square

Table 1. Location and general description of experimental areas

Locality	Approximate acreage	Soil	Forest type (trees in order of abundance)	Age (years)	Grown density	Depth of litter
Brewster, Mass.	90	Coarse sand	Pitch pine, scarlet oak, white oak	60	0.4–0.6	Shallow
Freetown, Mass.	220	Sand	Scarlet oak, white oak, white pine	35–50	0.4–0.6	Shallow
Alfred, Me.		Sand	White pine, white oak, black oak	70	0.7–0.8	Shallow
Tract 1d	120					
Tract 1e	37	Sand	Black oak, white oak, white pine	45	0.5–0.6	Shallow
Wendell, Mass.	60	Sandy loam	Scarlet oak, white oak	45	0.6–0.7	Shallow
North Reading, Mass.	100	Loam	Red oak, white oak, red maple	60	0.6–0.7	Medium
Hillsborough, N.H.	65	Fine sandy loam	Red oak, paper birch, red maple, white oak	60	0.6–0.8	Medium
Petersham, Mass.						
Tract A[1]	250	Fine sandy loam	Red oak, gray birch, aspen	60	0.5–0.8	Medium to deep
Tract B	80	Fine sandy loam	Red oak, paper birch, red maple, white oak	30–35, 70	0.8–1.0	Deep

Northampton, Mass.	80	Fine sandy loam	Red oak, paper birch, white oak black birch	40–60	0.6–0.8	Medium
Spencer, Mass.	50	Fine sandy loam	Red oak, red maple, white oak	25–35	0.8–1.0	Deep
Eastford, Conn.	1,000	Fine sandy loam	Red oak, white oak red maple, hickory	60	0.7–0.9	Deep
Granby, Conn.	13 one-acre plots	Sandy loam	Red oak, white oak, red maple, hickory	60	0.6–0.8	Medium to deep
Burrillville, R.I.	105	Fine sandy loam	Red oak, white oak, red maple	50–60	0.8–0.9	Deep
Hillsdale, N.Y.	60	Sandy loam	Red oak, white oak red maple, chestnut oak	50–60	0.8–0.9	Medium to deep
Canaan, N.Y.	67	Sandy loam	Red oak, paper birch, white oak, black birch	50–60	0.8–0.9	Medium to deep
Pittston, Pa.	73	Loam	White oak, chestnut oak, red maple	35–40	0.6–0.7	Medium
Jenkins, Pa.	66	Loam	Red oak, white oak, red maple	45–60	0.8–0.9	Medium to deep

[1] Destroyed by 1938 hurricane.

plots were established. In all plots the egg mass population, egg mortality, hatch, and pupal population and mortality were followed closely each year. Periodically during the larval period collections of larvae were also made nearby each plot to obtain data on abundance, parasitization, and mortality caused by carabid beetles and microorganisms. The circular plots were marked with a center stake and the one-acre square plots at Granby with corner stakes.

Population and Mortality Measurements

In the intensive study plots estimates were obtained of the population and mortality in each developmental stage, however, some of the estimates of the population were indirect, rather than direct measurements. The population and mortality during the egg stage, and the population at the beginning of the first larval stage, could be readily determined with a high degree of accuracy from the egg mass populations, and the data on egg mass size, egg mortality, and hatch per mass obtained from the egg mass collections. It was also possible to obtain direct measurements of the larval mortality, pupal population, pupal mortality, male and female adult population, and the egg mass population, which represented the productive female population. By combining these data with the daily larval mortality data, estimates were obtained of the population and mortality on a daily basis during the larval period. The methods used in obtaining the basic data for the estimates in the different stages are discussed more fully below under the stages involved.

Egg

Each female moth within a few hours after emergence usually lays all of her eggs in a single mass and covers the mass with buff colored scales from her body. The eggs are laid in late June and July on the trunks and limbs of trees and on loose stones and debris. However, as stated above, the areas selected for plots were free of stonewalls, excessive debris, and old residual trees that might contain cavities attractive for pupation and egglaying, so that most egg masses laid within the plots were on tree trunks. The newly-laid egg masses were conspicuous and could be readily seen in the fall after the deciduous leaves had fallen before snow covered the ground.

The one-fifth acre intensive study plots and the one-tenth and one-acre supplementary plots were carefully examined throughout each fall and a complete tally made of the egg masses present. Estimates of the population within an area of approximately 5½ acres immediately surrounding each of the one-fifth acre intensive study plots were obtained by cruising the areas on compass lines 50 feet apart, and at 50-foot intervals on these lines counts were made of the egg masses found within sample areas, 10 feet by 10 feet square and extending to the top of the trees. In the larger experimental areas, usually 50 to 100 acres in size (one, however, contained 1,000 acres), the cruise lines were 200 feet apart and the sample areas examined were taken at 200-foot intervals on the lines.

The size of the egg masses for each plot was estimated on the basis

of data obtained from egg masses collected in the immediate vicinity of each plot. Just prior to hatching in the spring a spot collection of 6 to 10 egg masses were usually collected 75 to 100 feet from each of the 4 corners of each plot, or a total of 24 to 40 egg masses per plot. The egg masses were placed in individual vials or boxes and held inside the standard weather instrument shed in or near the plot until hatching was complete. When the population was low, the young larvae were removed at 1 to 2 day intervals, counted, and released at the approximate points where the egg masses were collected. After hatching was completed, the unhatched eggs were carefully "rubbed out" by hand on a piece of taut cheese cloth, which eliminated the scales and delicate shells of the hatched eggs. Then the non-hatched eggs were examined under a dissecting microscope and classified as to probable cause of death. Eggs killed by low winter temperatures contained fully-developed larvae which had a characteristic appearance, while parasitized eggs either had a parasite larva or adult within, or an emergence hole and debris within if the parasite had emerged. There were also a few of the non-hatched eggs which failed to undergo embryonic development or were dead from other unknown causes.

Larva

The hatch per egg mass, coupled with the egg mass populations within the plots, was used as the basis for estimating the initial larval population in the plots each spring. As soon as hatching began either 1 or 2, depending upon the population present, cloth-bottomed trays, 3 feet by 3 feet inside measurements, were placed flat on the ground at random within each of the 36 squares within each plot. The trays were carefully examined daily throughout the larval period, usually from about May 1 to July 31, and the number and instar of both living and dead larvae on them recorded. The living larvae were left undisturbed on the trays, however, the dead larvae were removed. Wilted larvae and those partially consumed by *Calosoma* beetles were recorded and eliminated. The others were retained and later examined and dissected under a dissecting microscope to determine the cause of death. After the generation was completed and the resultant egg masses counted, these estimates of the larval mortality were used along with those of the adult and pupal populations in estimating the larval population day by day and within each instar. This is discussed more fully in a later section.

In addition to the tray data, larval collections were made around each plot at approximately 2 week intervals during June and part of July to obtain supplemental information on the larval population and parasitization. The larvae were collected at a specific distance from the plot boundary from each of the 4 sides of the plot, similar to the egg mass collections, but different distances were used on each collection date. All larvae found by moving in a spiral manner around each collection point were collected until the desired number was obtained and then the time and approximate area traversed were recorded. The larvae were later dissected for parasite records. The larval collections made around the several widely distributed supplementary study plots were made in a similar manner.

Pupa

Two methods were used to procure estimates of the sex ratio, pupal population, and pupal mortality. In one the pupae and pupal skins in parts of the plots and sample areas outside the plots were examined to determine the pupal population and mortality per unit of area. The other entailed the examination of only the readily accessible pupae in parts of the plots and sample areas outside the plots to obtain data on the proportion of dead to living or emerged pupae. These examinations were usually made about the first of August when emergence was practically complete while the pupal skins were still fresh. The second method proved to be more practical than the former one, because of the difficulty of finding all pupae within a sample area, especially where tall trees were involved. From these data and the actual egg mass populations produced within the plots, the pupal populations and mortality could be estimated.

Adult

The number of female moths which emerged and lived to deposit their eggs was measured with a high degree of accuracy since the egg masses were conspicuous and each plot was carefully examined throughout for egg masses. Each female usually deposited her eggs in a single mass or cluster on or within a few inches of the empty pupal skin, therefore, estimates of the ratio of egg masses to emerged female moths and of male moths to egg masses were obtained from the examinations of pupal skins. These ratios were then used with the egg mass population data to obtain estimates of the male and female adult populations.

Defoliation Measurements

At the height of defoliation in July each year a reconnaissance was made throughout the study areas, and if there were any trees estimated to be 25 per cent defoliated, a systematic survey was made to obtain estimates of the degree of defoliation. In making these surveys a complete tally was made of the trees in the intensive study plots and in randomized one-tenth acre sample plots within the larger experimental areas, and an ocular estimate of the percentage defoliation was made of the trees individually by species and diameter classes at 2-inch intervals. The 9 divisions of defoliation used were made on a geometric basis around the 50 per cent median point and were as follows: 0, 6, 12, 25, 50, 75, 88, 94, and 100. It can be seen that there would be twice as much foliage left at 75 as at 87.5, and twice as much left at 50 as at 75. In a similar manner, there would be twice as much foliage removed at 25 as at 12.5, and twice as much removed at 50 as at 25. The defoliation data were transformed into terms of basal area, on the assumption that basal area was a usable index of the volume of foliage.

RESULTS

Fluctuations in the Population Density of the Moth from Year to Year

The most reliable measurements of the fluctuations in the abundance of the moth from year to year were based on egg mass counts made in the fall when they were conspicuous and could be counted with a high degree of accuracy. Since each moth normally laid all of her eggs in a single mass, the egg mass population was a good measure of the effective female moth population.

The yearly estimates of the egg mass populations within the larger experimental areas are shown in Table 2. The predominantly higher populations in certain areas (Alfred, Brewster, Freetown, Wendell) and low populations in others (Burrillville, Eastford, Granby) were in line with expectation from the overall defoliation records for the preceding decades (Brown and Sheals, 1944) which were considered to be indicative of the susceptibility of the woodlands from a regional standpoint. These studies revealed that there was relative stability of the populations within these specific woodlands and that the densities were probably representative of those that have prevailed within the different regions since the moth became established. For example, the populations in the Freetown area fluctuated between approximately 1000 and 3000 egg masses per acre for 4 years, 1941-1944, and those in the 13 acres that made up the Granby plots fluctuated between 0.7 and 7.0 egg masses per acre for 5 years, 1940-1944, with a maximum of 9 egg masses within an individual 1-acre plot. Another conspicuous aspect of the population fluctuations was the major general increase in the Northeast in 1944, and to a somewhat lesser extent in 1943, which suggests that from a regional standpoint ecological conditions were unusually favorable for increased survival in most of the areas in those years. In fact, the only exception in 1944 was the Brewster area where the population was sufficient to cause widespread defoliation and many larvae died of starvation in late June and July of 1944. Despite the large standard errors of several of the population estimates, the measurements were probably adequate for the purposes for which they were used. The causes which made it difficult to procure statistically good estimates of the egg mass populations throughout woodlands of appreciable size which have considerable ecological variability will be evident after consideration is given to the mortality data presented in later sections.

The egg mass populations within the 1/5-acre and 1/10-acre study plots which, like the 13 1-acre Granby plots, were examined carefully throughout each fall to obtain a complete count of the egg masses, gave relatively precise information on the fluctuations in the populations from year to year within these specific areas. The fluctuations within the 1/5-acre plots (Table 3) which were located in woodlands of relatively high susceptibility to the moth, as well as those in the 1/10-acre plots throughout the Northeast, gave a similar picture of population fluctuation as that given by the populations within the larger experimental areas. Since the population counts within the individual plots can be used with much greater confidence than the sample estimates

Table 2. Estimated egg mass populations within the experimental study areas

Locality	Approximate acreage	Number of egg masses per acre[1]								
		1936[2]	1937	1938	1939	1940	1941	1942	1943	1944
Brewster, Mass.	90						325±13	550±85	6300±800	160±65
Freetown, Mass.	220		700±110	12±6	7±5	250±35	950±160	3150±300	1400±300	2200±460
Alfred, Me.										[3]
Tract 1d	120			900±450	270±10		35±15	20±5	115±30	
Tract 1e	37			3100±370	430±90	230±40	15±10	40±15	45±17	320±80
Wendell, Mass.	60						1100±140	1360±130	1000±135	5600±500
No. Reading, Mass.	100						415±75	90±25	220±40	1200±135
Hillsborough, N. H.	65						80±40	110±35	195±20	[3]
Petersham, Mass.										
Tract A[4]	250	640±110	410±60							
Tract B	80			250±50	5±5	0[5]	10±8	40±20	950±425	5500±900
Northampton, Mass.	80						40±13	95±25	435±90	7900±1000
Spencer, Mass.	50						9±9	0	9±9	70±25
Eastford, Conn.	1000	0	0	0	0	0	0	0	0	0
Granby, Conn.	1000				640±145	5.9±.8	2.3±.6	1.9±.7	0.7±.3	7.0±2.7
Burrillville, R. I.	105						0	0	0	0
Hillsdale, N. Y.	60							0	11±8	120±38
Canaan, N. Y.	67							7±7	20±10	115±48
Pittston, Pa.	73							0	14±3	50±36[6]
Jenkins, Pa.	66							0	0	25±4

[1] Number of egg masses per 100 sq. ft. sample, multiplied by 435.6.
[2] Year eggs were deposited.
[3] Observations in these areas indicated a considerable increase over the 1943 populations.
[4] Forest severely damaged by 1938 hurricane.
[5] All zeroes indicate that no egg masses were found in the samples but there may have been a few present.
[6] There were approximately 300 egg masses on a large white oak in the area.

Table 3. Fluctuations in the egg mass population within the 1/5-acre study plots

Locality and plot	Number[1] of egg masses within the plots									
	1936[2]	1937	1938	1939	1940	1941	1942	1943	1944	1945
Petersham, Mass.										
HA	136	124	5							
HB	223	33	2							
HC	208	18	2							
HD	478	79	0							
H1			62	0	0	0	4	23	576	366
H2			105	0	3	1	0	5	783	46
H3			49	1	0	5	3	116	2,958	519
Oak						16	7	1	5,031	45
Gray birch						86	363	1,498	16	288
Freetown, Mass.										
FA		435	13	6	145	409	755	531	121	80
FB		446	16	6	225	394	501	86	238	388
FC		323	24	19	246	647	16	38	26	139
Woodstock, Conn.	72	321								
Alfred, Me.										
N					99	12	9	32	408	
S					21	0	1	2	22	
Wendell, Mass.										
N						195	196	184	1,135	244
S						236	229	219	1,007	530

[1] A complete tally was made of the egg masses.
[2] Year eggs were deposited.

for the larger experimental areas, the former have been used as the basis for the more detailed studies of the changes in population densities. With few exceptions, the population densities and trends (increase and decrease) within the individual plots at each locality were remarkably similar each year (Table 3). To facilitate discussion, 160 egg masses per 1/5-acre plot (800 per acre), has been considered as economic zero. The population density within the Freetown plots was above this point 7 out of 9 years, and in the Wendell plots 5 out of 5 years. Economic zero was exceeded only twice in 8 years in the Petersham plots (H series) and not once in 7 years in the Granby plots. When these populations are considered from the viewpoint of *rate of change* by dividing the population produced by the spring population (Figures 1 and 2) it becomes evident that there was no clearcut relationship between population density and rate of increase. The rates of increase and decrease were *lower* and *more* stable in the Freetown and Wendell plots where populations above economic zero predominated than in the Petersham plots where this population density was not reached. These data, as well as those obtained in the 1/10-acre plots located in the several experimental areas, showed that at the lower population densities rate of increase and decrease varied a great deal. In terms of actual numbers these variations at relatively low densities were of course less than those in the Freetown plots where relatively high densities predominated and there was considerable stability in the populations when considered from the viewpoint of rate of change.

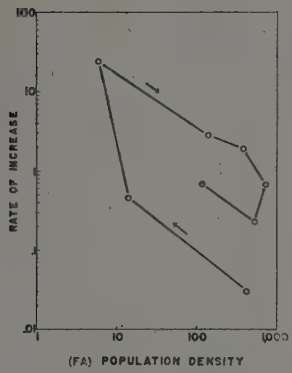
A number of other things such as number of eggs per mass, sex ratio, and defoliation were often clearly related to the egg mass population density despite the variations in survival due to weather and other ecological factors. For example, in the summer of 1942 when there were sufficient numbers of larvae in the Freetown plots to cause appreciable defoliation and some starvation occurred, small moths were produced and the egg masses laid by them contained fewer than 200 eggs per mass (Table 4). In contrast, in the summer of 1940 when the

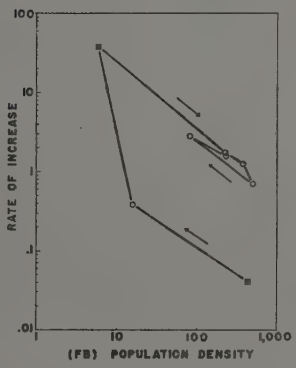
Table 4. Estimated size of the egg masses and hatch in the Freetown plots

	Number of eggs per mass							
Plot	1937[1]	1938	1939	1940	1941	1942	1943	1944
	Size of Egg Masses							
FA	250±20	260±45	500[2]	520±25	380±35	195±16	345±30	118±12
FB	280±15	240±25		540±20	230±20	145±12	455±20	510±38
FC	210±15	330±25		560±20	260±20	150±17	630±40	
	Hatch							
FA	150±25	150±40	330[2]	410±30	220±35			
FB	190±15	140±15		420±20	160±20			
FC	140±15	200±20		430±20	150±20			

[1] Year egg masses were deposited.

[2] Due to the scarcity of egg masses, only 31 egg masses were collected around all 3 plots and they were used as one sample. Faulty handling at the time of hatching resulted in the loss of several larvae, so that the estimates of the size of the masses and the hatch were not actually determined but the above figures are not far from the true figures.





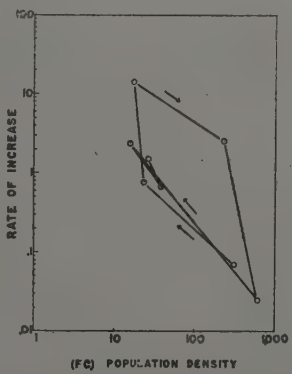
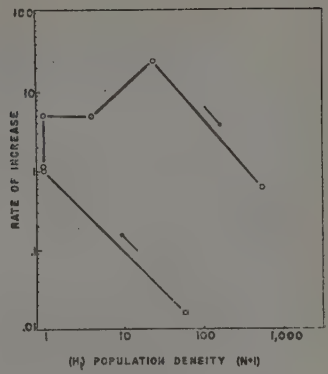
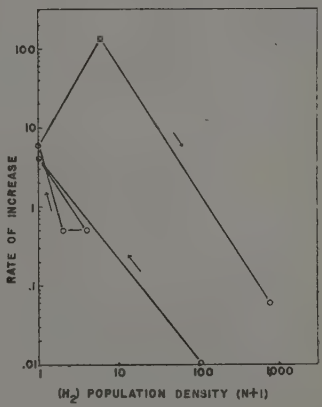


Figure 1. Rate of increase of the egg mass populations within the Freetown plots, 1937-45





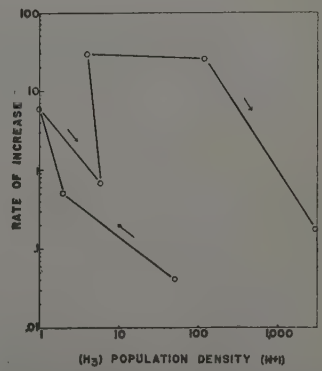


Figure 2. Rate of increase of the egg mass populations within one series of the Petersham plots, 1939-45

larval populations within these plots were relatively low, the egg masses produced contained over 500 eggs per mass. There were also localized variations in the size of egg masses which were commonly related to population density (Table 5). Similarly, the sex ratio was often inversely related to population density. In the summer of 1940 the number of female moths exceeded male moths by 3 to 1 in these plots, while in 1942 the number of males exceeded the females. As mentioned above, when there was 25 per cent or more defoliation of individual trees an estimate was made of the defoliation of each tree within the plots and used with the basal area in the calculation of the final estimates of defoliation. From these data it was found that at population densities of approximately 160 egg masses per 1/5-acre plot, or 800 per acre, defoliation seldom exceeded 25 per cent. Populations of around 400 per plot usually caused about 50 to 75 per cent defoliation and populations in excess of 600 often resulted in more than 90 per cent defoliation. On the other hand, there was very little defoliation in the Freetown plots in the summer of 1943 even though 2 of the plots had populations in excess of 500 egg masses each. However, the preceding winter had a prolonged period of sub-zero temperatures which killed about 90 per cent of the overwintering population.

Mortality in the Different Developmental Stages

Being a univoltine species, each year the populations were highest during the egg stage and became progressively less in each developmental stage until the adult stage. The duration of the different stages was approximately as follows: Egg, 9 to 10 months; larval, 60 to 90 days; pupal, 10 to 14 days; and adult females, 2 to 5 days. Therefore, on the basis of both numbers and the length of exposure to mortality factors, the mortality potential was much greater in the egg stage than in the other developmental stages.

Egg

Data obtained from the egg mass collections made immediately prior to hatching each spring provided estimates of the non-hatched eggs per mass, as well as the size, hatch, and parasitization per mass. These estimates were then combined with the egg mass counts to place

Table 5. Variation in the size of egg masses from different sides of the Freetown plots, spring 1938

Side of plot	Mean number of eggs per mass		
	FA	FB	FC
North	374.3±45.8	267.9±17.0	156.8±24.3
East	287.5±23.2	319.8±37.3	135.4±20.8
South	118.8±16.5	286.4±36.7	205.8±17.7
West	232.7±33.2	248.1±39.3	314.8±26.5
	255.3±41.3	282.6±15.8	213.2±16.5

Table 6. Egg mortality in the Freetown plots

Plot	Number of eggs per mass				
	1938[1]	1939	1940	1941	1942
FA	100±10	100±10		110±15	160±25
FB	95±5	100±10	170[2]±15	120±10	70±10
FC	75±5	120±10		140±10	110±15

[1] Spring following year when deposited.

[2] Due to the scarcity of egg masses, only 31 egg masses were collected around the 3 plots and these were used as one sample.

them on a plot basis. The egg mortality including those eggs killed by parasites, in the Freetown plots for the 5-year period, 1938-42, is shown in Table 6. Each year of this period appreciable numbers of eggs within these plots failed to hatch, with approximately 30-40 per cent mortality of the populations. The non-hatch was about 7 to 8 per cent in Petersham and Woodstock in the spring of 1937 and around 20 per cent in a number of instances in other areas. Except for the high egg mortality in localized areas in central and northern New England in the spring of 1943, egg mortality was less than 50 per cent from 1937 to 1945 in all areas where egg mass populations were obtained.

Larval

The estimates of the larval mortality were based on the dead larvae removed from the trays daily as is illustrated by the data obtained in the Freetown plots (Table 7). A further breakdown of the 1938 data by instars (Table 8) shows that there was appreciable mortality in each instar and that even in terms of numbers the mortality in the later instars was relatively high despite the populations being less than in the earlier instars. This is also illustrated indirectly by the survivorship curves which present the estimated populations within the different developmental stages in the individual Freetown plots for the 5-year period (Figure 3). A decided drop usually occurred in these larval populations during the 4th, 5th, and 6th instars, and on a percentage basis the mortality was especially conspicuous among these

Table 7. Mean number of dead larvae removed from the trays within the Freetown plots

Plot	Number of dead larvae recovered per tray[1]				
	1938	1939	1940	1941	1942
FA	36.44±1.56	0.65±.09	1.93±.25	11.33± .96	21.94±1.46
FB	60.75±3.91	0.81±.13	0.86±.12	18.56±1.22	27.25±1.84
FC	47.56±1.93	0.75±.11	1.35±.15	14.17± .92	32.89±1.55

[1] Based on total number of larvae removed from the trays during the season.

Table 8. Number of different instar larvae removed from the trays in the Freetown plots in 1938

Instar	Plot number		
	FA	FB	FC
First	306	321	398
Second	268	207	169
Third	179	335	392
Fourth	343	995	589
Fifth & Sixth	221	336	170
Total	1317	2194	1718

larger larvae (Table 9). In the better mesophytic forests the mortality among the larger larvae was considerably higher than in the Freetown area, as was shown by the larval liberation data and other evidences presented in an earlier paper (Bess *et al.*, 1947).

Supplementary data obtained from the more generalized measurements of larval populations and mortalities based on collections of living larvae made at 2-week intervals during the latter part of the larval period in the several widely distributed experimental areas provided a similar but less detailed picture of the progress of events. The limited number of samples and the few larvae obtained even by 3 hours of searching in some experimental areas, were insufficient to give adequate estimates of the populations and mortalities. However, at low population levels the data provided worthwhile measures of the relative abundance of the larvae in the different instars, as well as useful information on parasitization.

Pupal

Pupal mortality was far less than during the larval period (Table 10 and Figure 3). This was true on a percentage basis as well as in terms of absolute numbers.

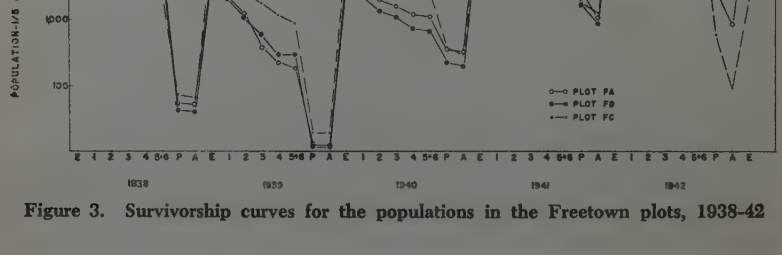


Figure 3. Survivorship curves for the populations in the Freetown plots, 1938-42

Table 9. Mean percentage apparent mortality in the different developmental stages in the three Freetown plots, 1938-1942

	1938	1939	1940	1941	1942	5-year mean
Egg	36.4	39.6	33.7	26.2	37.1	34.6
1st	20.3	47.1	28.2	21.2	11.2	25.6
2nd	16.8	48.9	18.4	23.0	9.1	23.2
3rd	26.0	42.1	27.4	31.8	14.0	28.3
4th	70.9	13.4	8.4	32.6	28.5	31.2
5th and 6th	99.2	95.7	73.1	90.3	92.8	90.2
Pupa	8.3	0	14.2	34.6	71.0	25.6
Total	99.4	99.4	94.0	99.1	99.2	98.3

Adult

The mortality of adult females prior to oviposition was found to be exceedingly low in all plots throughout the study. Furthermore, no egg mass was found that did not contain fertile eggs, which indicated that there was always an adequate male moth population. However, there was considerable variation in the sex ratio, which probably had an important influence on the population dynamics of the species. In the Freetown plots the sex ratio varied from as high as 3 females to 1 male to only 1 female to 6 males (Table 10).

Table 10. Estimated mortality and sex ratio of the pupae, and the sex ratio of the adults, in the Freetown plots (population was too low to procure adequate samples to obtain reliable estimates in 1939)

Plot	Year			
	1938	1940	1941	1942
	Percentage of pupae examined that failed to emerge			
FA	7.0 ±2.6	11.8 ±2.2	47.7 ±3.2	59.2 ±3.3
FB	7.4 ±2.8	10.3 ±2.2	27.9 ±3.2	69.6 ±3.1
FC	11.1 ±3.5	20.7 ±2.2	28.3 ±4.7	84.2[1] ±2.3
	Sex ratio of pupae examined			
FA	0.31± .05	0.75± .03	0.50± .03	0.30 ± .03
FB	0.33± .05	0.72± .03	0.38± .03	0.49 ± .03
FC	0.38± .05	0.77± .02	0.50± .05	0.17[1]± .02
	Percentage of the emerged pupal skins examined that were males			
FA	67.4 ±5.0	25.9 ±3.1	48.0 ±4.5	38.0 ±5.2
FB	68.4 ±5.2	28.0 ±3.5	62.0 ±4.1	39.7 ±5.9
FC	61.6 ±5.7	25.6 ±2.7	55.2 ±3.6	76.9[1] ±6.8

[1] Heavy stripping occurred in this plot, causing considerable starvation of the larger larvae.

Estimated Mortality Caused by Different Factors

Estimates of the mortality caused by different factors may be compiled and considered in a number of different ways. Since the dead larvae were removed from the trays daily it was possible to compute the larval mortality on that basis as well as by instars.

Compilation and analysis of the data on a daily basis made it possible to detect catastrophic effects attributable to the direct and indirect effects of weather. This approach appeared to be more cumbersome and perhaps less useful than presentation on the basis of the mortality in the different developmental stages. There was also the question of whether the mortality should be presented and discussed on the basis of the *numbers* that died, *real mortality, apparent mortality,* or all three. Apparent mortality has been emphasized; however, a good deal of information on the numbers that died and real mortality was included.

Physical Factors

Low temperatures and driving rains were the only physical factors observed to cause appreciable direct mortality; however, a number of elements of weather and site influenced mortality indirectly. The mortality from these indirect effects could not be measured quantitatively.

Summers (1922) concluded that about 50 per cent of the eggs were killed at −15°F., and that all eggs were killed at −25°F. As is true with many insects, unseasonably low temperatures in the fall or spring were found to cause more mortality than similar temperatures in midwinter. However, the only extensive mortality from low temperatures that occurred in the experimental areas during the period of study (1936-45) was caused by sub-zero mid-winter temperatures. At temperatures slightly below zero relative elevation and air drainage had an important effect on the extensiveness of mortality due to low temperatures. The temperatures were lower and the mortality greater in the relatively low areas, or frost pockets, than in the relatively high areas. Snow provided protection against sub-zero temperatures and winter mortality. In the colder areas of New England and New York probably most of the eggs above the snow line are usually killed by the low winter temperatures that commonly occur in these areas. Approximately 90 per cent of the eggs in the Petersham plots and 10 per cent of those in the Freetown plots were killed during the winter of 1937-38 by sub-zero temperatures which occurred on and immediately after January 20. Even more extensive winter kill occurred in southern New England during the winter of 1942-43 when around 80 per cent of the overwintering gypsy moth eggs within the Freetown plots were killed. The mortality of the overwintering parasite larvae within the gypsy moth eggs was higher than that of the gypsy moth larvae. Occasionally during heavy rainstorms caterpillars were dislodged from the foliage and apparently drowned on the ground. This probably occurred more frequently during spring storms when the caterpillars were still small; however, in one particularly heavy rainstorm in June, dozens of large caterpillars were killed in the above manner.

As has been pointed out by Bess *et al.* (1947), rainfall, fire, soil,

and other factors that influence site conditions also affect other factors that cause mortality. The indirect effects of some of these factors are discussed in conjunction with the biotic factors involved.

Biotic Factors

Inherent Attributes of the Species

The inherent characteristics or attributes of the gypsy moth, from the standpoint of physiology, structure, and habits, play an important role in the mortality, survival, and abundance of the insect. It was not possible to get estimates of the mortality caused by such factors but it was deemed desirable to at least point out that some of the mortality might be attributed to weaknesses of the species itself, rather than to physical factors or other biotic factors.

Some of these weaknesses might be classed as physiological or structural. For instance, hundreds of egg masses were examined during this study and all of them contained fertile eggs. However, there were always a few eggs, usually less than 5 per cent, in each egg mass which failed to undergo embryonic development. Invariably, there were some larvae that died from unknown causes in the plots every day during the larval period. Some of these died in the process of molting and the alimentary tracts of others were packed unusually tight with food material which the larvae had apparently been unable to eliminate. Dozens of moths died without emergence from the pupal skins and no apparent cause of death was detected. Individuals with structural abnormalities or defects were observed from time to time but there were relatively few of them.

There is little doubt but what larval behavior has an important influence on mortality and survival. The spinning habits of the larvae immediately following hatching is probably of considerable beneficial value to the species in dissemination but it is also the indirect cause of death of many larvae. For example, many of the young larvae are distributed to areas where there is no suitable food for them and they starve. Throughout the larval period apparently healthy larvae were continually dropping onto the ground and after a brisk wind, especially a shower acccompanied by wind, thousands of living larvae per acre were on the ground at one time. Obviously the increased hazards to survival resulting from this behavior vary with weather and forest conditions. The older larvae feed primarily at night and tend to remain during the day time in secluded places, such as are commonly available in the litter of mesophytic hardwood stands. Since predacious enemies of the larvae and pupae may be abundant in the litter of such stands, larval behavior indirectly influences mortality and survival.

In general, the development of the gypsy moth is well synchronized with the seasons in the northeastern United States, but there are a few divergencies which cause mortality from time to time. A few larvae may hatch during mild periods in the fall or winter and all of these die. In the more northern sections larvae sometimes break diapause and hatch so early in the spring that they are either killed by the low temperatures that commonly occur within these areas at that season, or they die from starvation. The observed mortality attributed in part to this weakness of species was discussed under physical factors.

Diseases

There was a non-filterable virus disease, known as "wilt" or polyhedrosis, which killed gypsy moth larvae and pupae. In some instances the disease becomes epidemic, especially in heavily infested woodlands when the weather is hot and humid.

It appeared that the larvae which fed on aspen (*Populus grandidentata* and *P. tremuloides*) in the Petersham plots in 1937 were more heavily infected with wilt than those which fed on oak (*Quercus rubra, Q. velutina*) foliage. For example, there was more wilt in Plot HA, which was composed largely of oak, than in the other Petersham plots which had less oak and more aspen in them. Furthermore, about one-half of Plot HB was largely oak and the other half largely aspen, and there were more wilted larvae recovered from the trays under aspen than from those under oak.

Wilt caused appreciable mortality of larvae in the Petersham plots in 1937 and the Freetown plots in 1938 (Table 11) but caused little mortality in these plots in other years or in the other study plots.

Predators

Many animals are known to be at least casual feeders on the gypsy moth, but it was difficult to procure reliable estimates of the mortality caused by them. A list of the known predators of the moth would include several species of birds, small mammals, spiders, ants, bugs, and beetles.

Quantitative estimates of the mortality typical of that caused by carabid beetles (*Calosoma sycophanta* L. and *C. frigidum* Kby.), were obtained from examination of the dead larvae recovered from the trays and the samples of pupae. However, the estimates of the larval mortality from this cause are conservative, especially where the ecological conditions were such that the larger larvae tended to spend the day time and molt on the forest floor. Under such conditions, beetle-killed larvae were commonly found in the litter near the bases of trees even where the larval population was relatively low. The above larval habits, which result in larvae becoming congregated in the litter near the bases of the trees throughout the day, make the larvae especially vulnerable to these predators when larvae are relatively scarce. It was found that enticement of the larvae to remain above the forest floor through the use of burlap bands on trees, as well as the exclusion of small mammals by hardware cloth enclosures, resulted in increased survival and reduced mortality from predators.

The measured larval mortality from predacious beetles obtained from the tray records and the pupal mortality through the pupal samples are summarized in Table 11.

Parasites

About 20 species of parasites of the gypsy moth have been imported from Europe and the Orient and liberated in New England (Burgess and Crossman, 1929). Five of the species liberated, 2 egg parasites and 3 larval parasites, have become sufficiently abundant at times to be considered important enemies of the pest in the Northeast. All 5 species were liberated

Table 11. Estimated mortality caused by different factors within the Freetown plots, 1938-42. Figures are on the basis of the per cent of the original population, or real mortality

Cause of mortality	1938	1939	1940	1941	1942
Low winter temperatures	10.2	2.3	4.2	2.4	10.9
Polyhedrosis	3.2	0	0.2	0	0
Calosoma beetles	13.2	0.1	5.1	1.6	12.8
Parasites	29.1	36.9	29.4	19.2	25.3
Undetermined (measured)	29.8	13.3	26.3	16.7	10.4
Unmeasured	14.5	44.0	26.3	59.1	39.8

over 40 years ago and from the start they showed evidence of their ability to survive and increase under New England conditions. However, each of the species, like their host, has usually been more abundant in some sections than others. One species may commonly parasitize a high percentage of its host in a section in which the host or one or more of the other parasites are seldom or never relatively abundant.

Anastatus disparis Ruschka. The egg parasite, *Anastatus disparis* Ruschka, destroys thousands of gypsy moth eggs every year in the eastern section of New England. It is quite hardy, successfully withstanding the winters of the northern portion of the region commonly heavily infested with the moth, which includes the southern part of Maine and the southeastern one-third of New Hampshire. In severe winters the overwintering parasite larvae within exposed eggs are frequently killed. Often 15 to 25 per cent of the eggs may be parasitized year after year in certain localities despite the relatively violent fluctuations in the host density. For instance, Crossman (1925) found that in experimental plots at Peabody, Massachusetts, during a period of 11 years, 1910-20, the minimum parasitization for any year was 17 per cent and the maximum 28 per cent. During the present study *A. disparis* was relatively abundant in the Freetown plots but varied a good deal in the Petersham plots and in the colder areas.

Oencyrtus kuwanae (Howard). The other imported egg parasite, *Oencyrtus kuwanae* (Howard), is widely distributed over most of the infested part of New England but it is seldom abundant in the colder sections of the infested region. Apparently the species is less cold hardy than *A. disparis*. It is commonly found in southern New England but has also been found to parasitize 20 per cent or more of the eggs in certain localities in the Connecticut River Valley in southern Vermont.

For the sake of brevity, the data on the parasitization by *A. disparis* and *O. kuwanae* were combined in the final tabulations. The minimum parasitization by these egg parasites in the Freetown plots from 1937 to 1942 was 17 per cent and the maximum 37 (Table 12). However, during the winter of 1942-43 low temperatures killed a high percentage of both the gypsy moth eggs and the egg parasites within these plots. The following season the parasitization dropped to approximately 7 per cent around the plots. In 1944 egg collections revealed that the parasitization had bounded back to about 30 per cent.

The information obtained on larval parasitization was far more difficult to present in a clearcut concise manner than that obtained on egg

Table 12. Comparison between apparent mortality and real mortality in the Freetown plots for 1938 and 1941

Stage	Apparent mortality			Real mortality		
	FA	FB	FC	FA	FB	FC
			1938			
Egg	40.7	38.8	34.8	40.7	33.8	34.8
1st	23.2	14.6	23.1	13.8	9.7	15.1
2nd	26.5	11.0	12.8	12.1	6.2	6.4
3rd	24.0	20.1	34.0	8.0	10.1	14.9
4th	60.7	74.6	77.4	15.4	30.0	22.3
5–6th	99.6	99.6	98.4	10.0	10.2	6.4
Pupa	7.0	7.0	10.8	0.0+	0.0+	0.0+
Total	99.96	99.96	99.91	99.96	99.96	99.91
			1941			
Egg	21.6	33.0	24.1	21.6	33.0	24.1
1st	23.0	19.5	21.2	18.0	13.1	16.1
2nd	23.8	24.8	20.5	14.4	13.4	12.3
3rd	33.1	34.8	27.5	15.2	14.1	13.1
4th	26.7	41.5	29.5	8.2	11.0	10.2
5–6th	90.4	85.5	95.0	20.4	13.2	23.1
Pupa	47.7	27.9	28.3	1.0	1.4	0.3
Total	98.87	99.15	99.14	98.87	99.15	99.14

parasitization for several larval stages were involved and the populations were different in each stage. Many of the caterpillars dissected contained 1 or more larvae of 2 parasites which further complicated the problem. It was deemed advisable to first briefly discuss the major parasites individually and then to summarize the total parasitization for all species.

Apanteles melanoscelus Ratzeburg. *Apanteles melanoscelus* Ratzeburg is a larval parasite which at times becomes quite abundant in certain localities. Frequently, 25 per cent of the second and third instar larvae present on a particular date may contain larvae of this parasite and there is commonly a second generation which attacks the later instars. In Freetown in 1938, where there was a fairly high larval population, collections indicated that over 50 per cent of the larvae on June 29 were parasitized by *A. melanoscelus*. The 2 generations each season increase the potentialities of the species to reduce the population of its host.

Compsilura concinnata Meigen. The larval parasite, *Compsilura concinnata* Meigen, can be found in large numbers every year in New England. In certain localities it becomes exceedingly abundant, and in a few instances over 80 per cent of the later instar larvae collected on a particular date contained maggots of this fly. The parasite has been more abundant in the mesophytic forests of southern New England and eastern New York than in the more xerophytic habitats of southeastern Massachusetts. Parasitization often exceeds 50 per cent in Connecticut and parts of Rhode Island. Several collections of larvae from eastern

New York in June of 1941 indicated that this fly had parasitized about one-third of the larvae present at the time the collections were made. Since it was active over a period of weeks when gypsy moth larvae were present, more than one brood was produced, and it often caused more mortality than indicated from a single collection.

Sturmia scutellata Robineau-Desvoidy. The third larval parasite, *Sturmia scutellata* Robineau-Desvoidy, has also been found throughout most of the infested region. However, like *C. concinnata*, it has not been important in the more xerophytic habitats in southeastern Massachusetts. It was extremely scarce in the Freetown plots throughout the period of study and was not abundant in any of the other plots. However, in some supplementary collections over 50 per cent of the pupae contained maggots of this tachnid.

Miscellaneous species. Occasionally a larva or pupa was found to be parasitized by one of the many miscellaneous species of parasites which have been bred from the gypsy moth in New England. In 1942 at Freetown a native parasite, *Theronia fulvescens* Cresson, parasitized about 18 per cent of the pupae around 1 of the plots. However, none of these miscellaneous species has been sufficiently numerous to be considered an important factor of control.

Some of the data on larval parasitization given in Tables 12 and 13

Table 13. Larval parasitization around the Freetown plots based on the dissection of living larvae collected on different dates from 1938 to 1943

Date collected	No. larvae in collections	Mean per cent parasitized[1]
1938		
June 3	1305	15.3± 3.5[2]
June 29	672	63.6± 9.5
July 21	231	13.1± 0.8
1939[3]		
June 8	167	52.3±12.9
1940		
June 13	264	1.4± 0.9
June 28	410	6.7± 2.9
July 17	115	14.6± 9.5
1941		
June 9	597	2.2± 0.6
July 9	205	18.9± 4.0
1942		
June 17	588	1.4± 0.1
July 1	302	5.3± 0.9
July 17	128	41.7±16.1
1943		
June 6	433	9.6± 6.0
June 26	388	5.9± 3.0
July 17	244	2.0± 1.0

[1] Based on the 3 plots.
[2] Standard error of the mean.
[3] Larvae too scarce to make additional collections in 1939.

show that appreciable parasitization occurred at times but that there was considerable variation from season to season and from one locality to another. The relatively high larval parasitization in the Freetown plots in 1938 and 1939, followed by 4 years of relatively low parasitization, illustrates the difficulties in attempting to use average figures. The fluctuations in larval parasitization in the Petersham plots were more violent, with high parasitization in 1937, low in 1938, high again in 1939, and low again in 1942. However, 3 different series of plots were involved due to the sporadic nature of the moth populations in the region. In the Woodstock, Connecticut, plot larval parasitization was 11.7±2.9 per cent on June 24, 1937 and 69.1±2.2 per cent on June 22, 1938. These violent fluctuations suggest that averages may be misleading and that more detailed treatment of the data may be necessary.

The estimates of the *combined* parasitization for the egg, larval and pupal stages within the Freetown plots (Table 11) indicate that there was appreciable parasitization throughout the period and that the variations from year to year were relatively low. Much of this was due to the parasitization caused by egg parasites. If considered on the basis of numbers parasitized, these egg parasites caused more mortality than the larval parasites. Nevertheless, the per cent parasitization of the larval population was often much greater than the per cent parasitization of the egg population.

Mortality Due to Undetermined Causes

As mentioned earlier, it was not possible to determine the cause of death for many of the larvae removed from the trays in the plots. Some of this mortality might well have been caused by inherent weaknesses, physiological disorders, unrecognized disease organisms, starvation, etc., or a combination of factors. The mortality from undetermined causes was usually high, especially if compared with the mortality produced by only one of the known factors (Table 11).

Evaluation of Ecological Factors Affecting Abundance

The data obtained within the special intensive study plots and the several larger supplementary experimental areas, plus the extensive field

Table 14. Larval parasitization around the Petersham plots as determined from the dissection of living larvae collected on different dates in 1939

Date collected	H1		H2		H3	
	No. larvae in collection	Per cent Para-sitized	No. larvae in collection	Per cent para-sitized	No. larvae in collection	Per cent para-sitized
June 9	412	31.1±2.3[1]	433	26.8±2.1	126	27.8±4.0
June 22	221	44.8±3.3	200	59.1±3.3	64	46.9±6.2
July 5	47	73.5±6.3	98	72.5±4.5	[2]	

[1] Standard error of the percentage.
[2] Too few larvae present to get a collection.

observations throughout the Northeast, revealed that the amount of mortality caused by different factors, such as diseases, predators, and parasites, usually varied a great deal from one locality to another and from one year to another. Nevertheless, each species, like the moth, tended to be more prevalent in one ecological region than in another.

The polyhedrosis wilt disease caused comparatively little mortality in the study areas during the period of study. Epizootics of this virus have been reputed to be associated with high population densities of its host; however, it appears likely that other factors, such as the quality or kind of larval food may affect the abundance of the virus. In the oak-pine woodlands on Cape Cod, the moth tends to persist at relatively high population densities year after year in the presence of the virus.

Predators caused a considerable amount of mortality among the larger larvae and pupae, especially in the more mesophytic woodlands with considerable litter. In such stands only a small portion of the mortality caused by predators was measured by the tray method. In some instances, sizeable numbers of larvae and pupae partially eaten or cut by *Calosoma* beetles were obtained in the mortality samples. The indirect measurements of mortality by the survivals from larval liberations and pupal placements gave convincing evidence of the high mortality caused by predators. Apparently the greater part of mortality by predation was caused by two small mammals, the short-tailed shrew (*Blarina brevicanda brevicanda* [Say]) and the deer mouse (*Peromyscus leucopus novebroracensis* [Fischer]), both voracious insect eaters, and two carabid beetles (*Calosoma sycophanta* L. and *C. frigidum* Kby.). The shrew and deer mouse were much more abundant in the better mesophytic woodlands prevalent around Petersham, in central Massachusetts, than in the more xerophytic woodlands in the vicinity of Freetown, in southeastern Massachusetts. Since the gypsy moth was commonly more abundant in the latter area, obviously the general abundance of these predators was not directly related to the general abundance of the moth. On the other hand, possibly within certain parts of New England, the abundance of *C. sycophanta* was directly related to the abundance of the gypsy moth but not in certain woodlands on light sandy soils on Cape Cod where the moth persists at high population densities. Other workers observed that in these light sandy soils the earthen chambers created by the *C. sycophanta* larvae prior to pupation and the adults prior to hibernation often collapsed resulting in high mortality of the beetle. *C. sycophanta* appeared to be generally most abundant in the central and western portions of the heavily infested zone where the soils tend to be sandy loams. It was not generally abundant in northern and western Connecticut where *C. frigidum* was frequently seen, even though the gypsy moth was seldom abundant in this region.

Each of the principal parasites also appeared to be relatively more abundant in one ecological region than in others, and in many instances the abundance of the parasites was not directly related to the abundance of the gypsy moth. However, within a particular locality, the abundance of the moth often had an appreciable influence on the actual abundance of the parasites and the numbers killed by them.

The productivity of the egg parasites was found to be directly related to the *relative* number of host eggs available to them (Figures 4 and 5). However, despite the excellent correlation on that basis, there

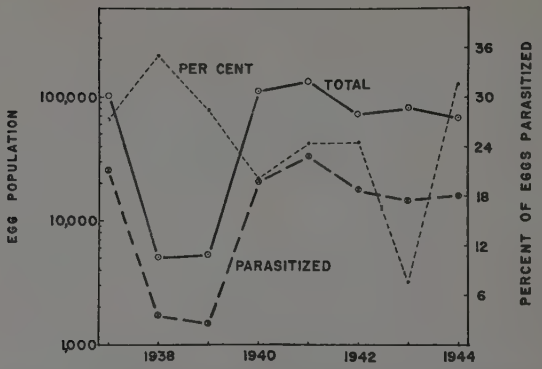


Figure 4. Total egg population, parasitized egg population, and per cent parasitization within Plot FA, Freetown, 1937-44.

appeared to be no relationship between percentage parasitization and the host egg population density (Table 15). This suggests that increased host abundance favored increased parasite abundance but not necessarily increased percentage parasitization. The percentage parasitization was inversely related to the number of host eggs available to the adult parasites (Figure 6). The highest egg parasitization observed during these studies was from northeastern Connecticut where the gypsy moth

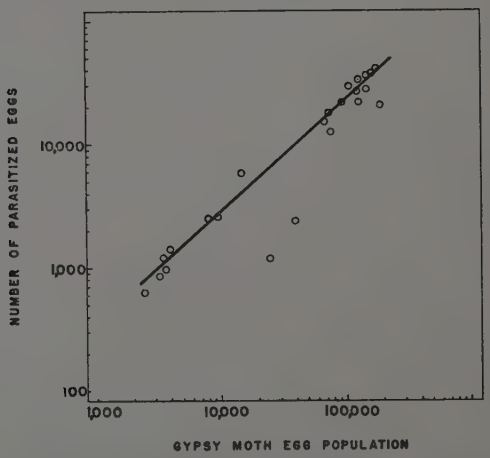


Figure 5. Relationship between the total egg population and parasitized egg population within the Freetown plots. The 3 points furthest from the line represent the population produced in 1943, the year following the heavy mortality that occurred during the 1942-43 winter.

Table 15. Egg population and parasitization around the Freetown plots

Year	Egg population (per 1/5 acre plot)	Per cent parasitized
1937	100,000	25.2
1938	5,000	35.0
1939	5,400	27.7
1940	113,000	18.3
1941	138,000	24.3
1942	74,000	24.3
1943[1]	104,000	7.3
1944	55,000	31.4

[1] Low winter temperatures in winter of 1942-43 killed a greater proportion of the overwintering egg parasites than of the gypsy moth.

population was very low and had been so for 3 years. At these low host densities a high parasite/host ratio is maintained. These parasites are considered to reproduce almost exclusively on gypsy moth eggs.

Two of the larval parasites, *A. melanoscelus* and *S. scutellata*, are also practically limited to gypsy moth larvae as hosts while *C. concinnata* develops successfully in many different species of lepidopterous hosts in the field. Abundance of these parasites was no doubt affected by the abundance of gypsy moth caterpillars; however, due to the multiplicity of interacting ecological factors the data failed to reveal conclusive evidence of such a relationship, even for the 2 species more or less dependent upon the moth as a host. *A. melanoscelus* was relatively abundant in the Freetown plots in 1938 when the host population was high and in the following year when the host population was low,

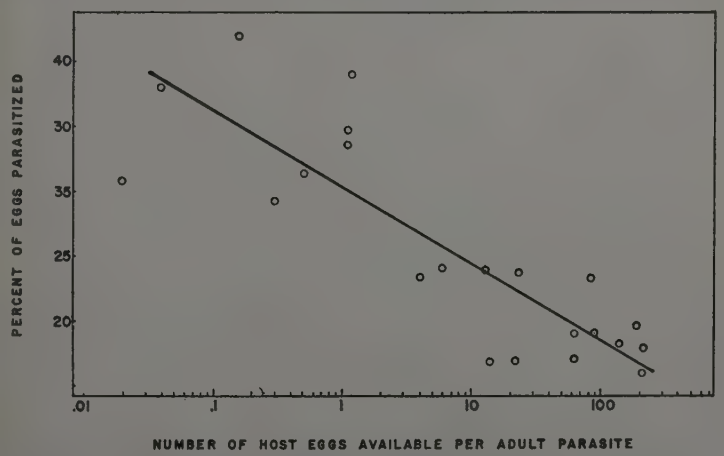


Figure 6. Relationship between parasitization and the number of host eggs available per adult parasite.

but was conspicuously scarce the following 4 years when the host was abundant. It behaved somewhat similarly in the Petersham plots. *S. scutellata* was relatively abundant in the Petersham plots in 1937 but was not encountered in numbers of consequence in other years or in any of the other plots. On the other hand, *C. concinnata* often parasitized 20 per cent or more of the gypsy moth caterpillars in many localities, especially in the better oak woodlands in Connecticut, Rhode Island, and central and western Massachusetts. Parasitization in excess of 60 per cent frequently occurs in certain localities where the gypsy moth has never been abundant. Perhaps the highest populations of this fly observed by the writer occurred in medium to heavy gypsy moth populations in Rhode Island and eastern Massachusetts. However, parasitization was conspicuously low in the several collections made on Cape Cod where the moth was abundant year after year.

Discussion

Many valuable contributions in the field of biological control and natural control of insect pests are available (Howard and Fiske, 1911; Thompson, 1928 and 1939; Thompson and Parker, 1928; Uvarov, 1931; Nicholson, 1933 and 1954; Gause, 1934; Nicholson and Bailey, 1935; Smith, 1935; Bodenheimer, 1938; DeBach and Smith, 1941; Varley, 1947; Ullyett, 1947; Solomon, 1949; Andrewartha and Birch, 1954; Harville, 1955; Milne, 1957; Morris, 1957; Morris *et al.*, 1958; and others) and a number of papers summarize different viewpoints concerning the importance of individual ecological factors. A review of these papers is not needed here but suffice it to state that no one is optimistic about the possibilities for precise assessment of individual factors in the regulation of population densities under field conditions.

The multiplicity of interacting dynamic factors which caused mortality of the gypsy moth within a woodland made it impossible to evaluate precisely the effects of these individual factors on the *reduction* or *regulation* of the population. In fact, there is no accepted method for even making a precise evaluation of the effects of such factors on the basis of their "relative importance" on the reduction of the population of the moth during a season. Since the mortality caused by one factor may influence that caused by another, parameters of the effects of such factors may be considered to be dynamic in character, similar to energy balance in climatology.

The possible effects of the death of one or more eggs, larvae, or pupae on the adult population produced may be considered from a number of viewpoints. One is from the viewpoint of the absolute numbers that died, such as is illustrated by survivorship curves (Figure 3). Another is to express the mortality as a percentage of the original or egg population, which has been commonly referred to as real mortality. A third is the mortality as a percentage of the population at the time when the mortality occurred, which is known as apparent mortality. A fourth approach which has not been widely used is to transpose the mortality into the mortality/survival ratio and thus express the mortality as odds against survival in contrast to per cent mortality which expresses it as the probability of death. The writer was assured by actuaries that the reasoning followed in the use of odds is "correctly

Table 16. Estimated reduction effect of the mortality in the different stages on the adult population in the Freetown plots, 1938-1942

Stage	Reduction coefficient (mortality/survival ratio)				
	1938	1939	1940	1941	1942
Egg	.57	.66	.51	.36	.59
1st	.25	.89	.39	.27	.13
2nd	.20	.96	.23	.30	.10
3rd	.35	.73	.38	.47	.16
4th	2.44	.15	.09	.48	.40
5th & 6th	124.00	22.26	2.72	9.31	12.89
Pupal	.09	0	.17	.53	2.45

along actuarial lines." It is suggested that the odds that prevailed against an individual's survival through a developmental stage, or as a result of a mortality factor, may be a useful index of the hazard or reduction effects of the mortality on the population. However, odds, like probabilities, are only approximations of the reduction effects on the adult population for a reduction in mortality within a particular stage may *either reduce or increase* the efficiency of a mortality-producing factor in a subsequent stage.

The hazards or odds against survival of the 5th-6th instar larvae within the Freetown plots were usually several times those in any of the other developmental stages (Table 16) and were even greater in the better mesophytic woodlands. Mortality within these instars was inversely correlated with the adult and egg populations produced (Figures 7 and 8), while there was no such correlation between the

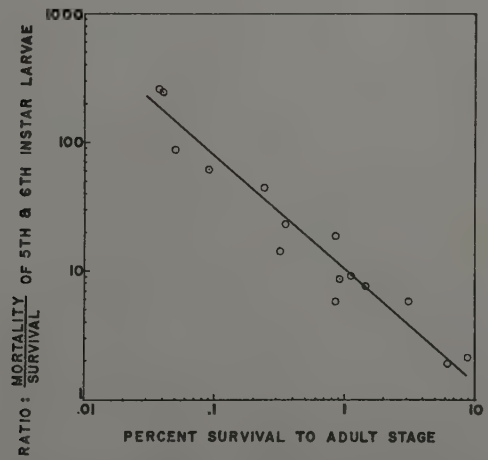


Figure 7. Relationship between mortality/survival ratios for 5th-6th instar larvae, and per cent survival to the adult stage.

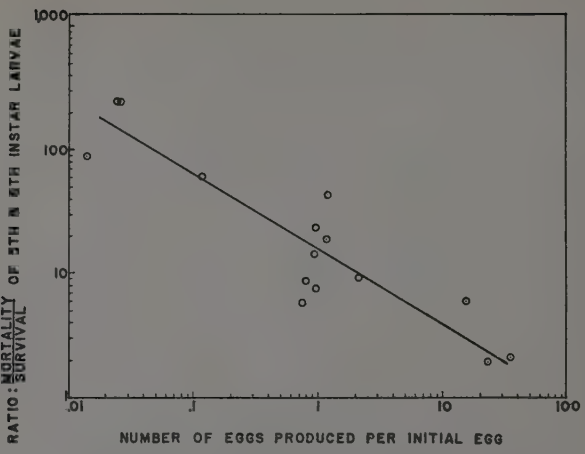


Figure 8. Relationship between mortality/survival ratios and the number of eggs produced per initial egg.

mortality in other stages with those populations. These data, and those obtained from the larval liberations and pupal placements (Bess *et al.*, 1947), indicate that the 5th-6th instars were the most hazardous developmental stages, and that the mortality of the larger larvae played a major role in determining the subsequent adult populations.

In an attempt to obtain estimates of the relative importance of the different groups of mortality factors the mortality/survival ratios for the mortalities were combined in the manner described by Bess (Bess, 1945). It can be seen from the data presented that the hazard attributable to the different ecological factors varied a great deal from year to year and from locality to locality. *Calosoma* beetles were of considerable importance in the reduction of the populations in the Freetown and Petersham plots but had little influence in the Alfred and Wendell plots. However, supplementary data obtained in woodlands in northern Connecticut and western Massachusetts where the moth was scarce revealed that the native species, *C. frigidium*, was

Table 17. Relative reduction effects of the mortality produced by different factors in the Freetown plots, 1938-1942

Cause of mortality	Reduction coefficient (mortality/survival ratio)				
	1938	1939	1940	1941	1942
Lower winter temperatures	.12	.04	.06	.03	.18
Polyhedrosis	17.29	0.00	.09	0.00	.11
Calosoma beetles	106.24	1.31	1.77	5.45	204.06
Parasites	28.42	1.67	1.22	1.91	2.72
Undetermined (inherent weaknesses, etc.)	316.08	155.81	5.44	25.59	7.40

usually an important factor in the reduction of the populations. Insectivorous small mammals were considered to be of key importance in the reduction of the populations in many mesophytic woodlands but the tray method did not measure this mortality. The reduction by parasites was important every year in the Freetown plots and in many other woodlands but usually not to as great an extent as predators. Parasites had an appreciable effect in the Petersham plots in 1939 but had relatively little effect in 1937, 1938, and 1942. Low winter temperatures were relatively unimportant in any of the plots during the years when quantitative data were obtained on the mortality in the different stages. However, they caused considerable mortality in the colder sections of the Northeast in the winters of 1937-38 and 1942-43. Polyhedrosis, similar to low winter temperatures, was erratic but occasionally caused appreciable mortality. The reduction by this disease was important in the Freetown plots in 1937 and again in 1938 but was unimportant in other years and in the other study areas.

The influence of an individual factor is seldom independent of that of others and in many instances the influences by two or more factors are exerted simultaneously rather than in sequence. This commonly results in parasitized or diseased larvae being killed by predators, even though they were destined to die from another cause. It is the sum total of all such influences during the season that determine the susceptibility of a woodland for the survival of the population present, which is of basic importance in respect to the density of the adult population and the progeny produced (Table 18).

Apparently the most effective entomophagous agents encountered were those which killed *relatively* high numbers in low moth populations, thus, tending to curtail or prevent increase, rather than causing a "crash" of high moth populations. It is quite possible that in many woodlands their efficiency tended to be inversely related to the population density of the moth. Parasite populations and the mortality caused by parasites within specific woodlands frequently increased with the population density of the host but percentage parasitization usually did not. It would appear logical to expect this with a parasite like *Compsilura concinnata* which had many other suitable hosts, especially in the Connecticut woodlands, but it also occurred repeatedly with the egg parasite, *Anastatus disparis,* which developed almost exclusively in gypsy moth eggs. A number of reasons might be advanced to support the postulate that a parasite should not necessarily be expected to exert the highest efficiency (per cent parasitization) at the highest host density, for food is only one of many physical and biotic components of the environment which influence a species either adversely or favorably.

Basically gypsy moth abundance or scarcity may be attributable to three things: the attributes of the species or population itself, the ecological conditions that prevailed in the woodlands, and the population density present that could respond to those ecological conditions. Many attributes of the species, such as the behavior patterns of the different instar larvae, indirectly affect survival. The ecological conditions within the woodlands in the Cape Cod area are usually favorable to survival and thousands of acres have been heavily defoliated annually for several decades. In this area literally millions of young gypsy moth caterpillars are disseminated by air currents each spring, resulting in

Table 18. Estimated egg and adult populations within the Freetown plots

Year & plot	Initial egg population	Adult population produced	Per cent survival	Egg population produced / Initial egg population
1938				
FA	108,800	40	0.04	0.03
FB	124,900	51	0.04	0.03
FC	67,800	63	0.09	0.12
1939				
FA	3,400	12	0.35	0.94
FB	3,800	12	0.32	0.92
FC	7,900	19	0.24	1.20
1940				
FA	3,200	196	6.12	23.56
FB	3,500	312	8.91	34.71
FC	9,500	291	3.06	15.09
1941				
FA	75,400	852	1.13	2.06
FB	121,500	1,037	0.85	0.75
FC	143,400	1,256	0.86	1.17
1942				
FA	155,400	2,246	1.45	0.95
FB	90,600	831	0.92	0.80
FC	168,200	92	0.05	0.01

many caterpillars being present in practically all woodlands. On the other hand, in western Massachusetts, the ecological conditions are usually unfavorable to the moth and even when they become temporarily favorable for one or more seasons there may be no caterpillars in them or nearby. Under good forest management with protection from fire, grazing, and similar abuses, many of the more susceptible woodlands outside of the zone where frequent heavy defoliation occurs may rapidly become less susceptible. On the other hand, highly susceptible woodlands on Cape Cod, many of which have been repeatedly subjected to defoliation and frequent burning, or to seasonal heavy use by campers, will require much more time and attention.

These intensive investigations, the widespread observations made throughout the Northeast in conjunction with them, and the past history of the insect in America and elsewhere, indicate that there is little likelihood that it will become a pest in good mesophytic woodlands, even though they are composed predominantly of favored food species. Furthermore, with the increased emphasis placed on forest management, which will reduce deterioration of woodlands due to burning, clearcutting, and grazing, this insect should become of increasingly less im-

portance. High crown density and deep litter within hardwood stands are conducive to a rich fauna, including predators which were found to be especially effective in preying on the larger gypsy moth caterpillars within such woodlands. Forest and site conditions apparently set the stage not only for the abundance of the moth but also for various enemies of the moth, and due cognizance should be given to them in control operations.

SUMMARY

Quantitative studies of the fluctuations in the population density and mortality of the gypsy moth in its different developmental stages were made within a number of woodland plots from 1937 to 1945. Detailed data on the populations and mortalities within the Freetown, Massachusetts, plots for 5 consecutive years, 1937-1942, were presented and these data used as a basis for much of the discussion within the paper. However, similar data from other intensive study plots located in Connecticut, Maine, and Massachusetts, as well as extensive data and observations within several additional study areas located in New England, eastern New York, and northeastern Pennsylvania, provided much supplemental information.

Survivorship curves for the populations within each of the Freetown plots over a 5-year period were given and many of the population and mortality data presented in different ways. The manner of presentation was a major problem since there was no accepted standard method available. Emphasis was placed on apparent mortality; however, the absolute numbers involved and real mortality were also considered important.

In an attempt to evaluate the mortality in one developmental stage on the final adult population produced, the mortality was converted into the mortality/survival ratio and used as an index of the relative reduction effect of the mortality. This ratio represented the odds against survival in contrast to per cent mortality the probability of death. It was concluded that the last larval instars were the most hazardous period in the development of the moth within the Freetown plots and even greater within more mesophytic woodlands.

In the evaluation of the mortality caused by different factors the mortality/survival ratio was also used as an index of the reduction effects of the mortality on the adult population produced. To make such assessments it was, of course, necessary to combine mortality/survival ratios. For example, the mortality/survival ratios for the mortality caused by parasites in each developmental stage—egg, 1st, 2nd, 3rd, 4th, 5-6th, and pupal—were combined into one figure in the sense of sequence, for the population density was different in each stage. It was concluded that forest and site conditions apparently set the stage for the abundance of the moth as well as for the various parasites and predators that preyed on it. Furthermore, the reduction effect exerted by a factor appeared to be more closely associated with the overall forest and site conditions than with the population density of the moth.

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